PHYSIOLOGICAL OBSERVATIONS ON WATER LOSS AND OXYGEN CONSUMPTION IN PERIPATUS [1]

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The small group of species which comprises the Onychophora have long been of interest because of their unique combination of arthropod and annelid characters which places them in a phylogenetic position intermediate to those two extensive groups (Snodgrass, 1938). They are further of interest because of their close homogeneity despite a sporadic distribution that encompasses a large portion of the world and points to an ancient separation of some of the genera (Clark, 1915; Brues, 1923). This homogeneity appears to be physiological and ecological as well as morphological,[2] since Peripatus is restricted everywhere to a moist but terrestrial environment. Further, their sporadic and fluctuating local distribution suggests that environmental variation, presumably in moisture, is actively limiting their occurrence even in the regions where they are found.

Physiological observations on members of this group, then, are of interest, and it is of particular interest to examine the process of water loss and to contrast Peripatus in this respect to comparable annelids and arthropods. Manton and Ramsay (1937) have reported a value for water loss in Peripatus (*Peripatopsis*) at 30° and with wind velocity of 7.0 m./sec. (16 m.p.h.). These conditions, however, seem rather severe for a species which is uncomfortable at temperatures above 20° (Manton, 1938) and which, living in crevices, must have little exposure to wind. The experiments reported here were made under conditions which more nearly approximate those encountered by the animal in nature.

In this connection reports in the literature suggest that there may have been some temperature adaptation in the Onychophora. Thus the two species studied here, both from Panama (lat. 9° N.), stayed in good condition at a temperature of 25° ±. In contrast as already noted, Peripatus from near Cape Town (lat. 34° S.) became uneasy at temperatures above 20° although low temperatures, even down to freezing, did not bother them. They survived very well in England (Manton, 1938; Sedgwick, 1885) as have specimens from New Zealand (lat. 40° S.). The latter were only successfully transported through the intervening tropical regions with the aid of refrigeration (Sedgwick, 1887). Peripatus from New Zealand (Hutton, 1876) and from Australia (Steel, 1896) are reported to become torpid during the winter but with no subsequent ill effects. On the other hand Sclater (1887) reported that his specimens from British Guiana (lat. 7° N.) successfully

[1] These observations are by no means complete, but because the literature contains little data on living Onychophora, particularly on New World species, and because there was no immediate prospect of obtaining a further supply of these unusual animals, it seemed advisable to present them at this time.

[2] It should be noted, however, that for such a small group of Onychophora show remarkable diversity in their embryological development and their mode of reproduction.

survived the trip to England, "but unfortunately were much affected by the cold, and were therefore killed."

Material

These Peripatus were secured on Barro Colorado Island, Canal Zone, through the great kindness of Mr. James Zetek. Two species (note Clark and Zetek, 1946) were obtained, the larger of which (*Epiperipatus brasiliensis varians*) had a contracted length of 50 mm. and was uniformly colored a rich red-brown. The smaller species (*Oroperipatus corradi*) had a contracted length of 25 mm. and was a chocolate color with lighter underside and with darker legs and a dark, median, dorsal stripe 0.3 mm. in width. The animals were taken in early September and these observations were made in Cambridge about a month later. During the interim they were kept in moist forest debris but were not given suitable food other than the supply of termites initially in the debris. The animals survived the trip well and apparently stayed in good health until just before death which presumably occurred through starvation.

The general behavior of these individuals corresponded to that described for other species (Manton, 1938; Holliday, 1942; Andrews, 1933; Steel, 1896; Sedgwick, 1885; etc.). They were retiring and preferred to remain inactive in some dark crevice. They are sensitive to light but react even more sharply to dryness which stimulates them to constant activity. The smaller species were definitely more sensitive in this respect and could not be held still even for a moment.

An occurrence involving an individual of the larger species may be of particular interest. On the occasion of mechanical injury to one of its antennae that member was placed in the mouth and the injured portion, about half the length, was removed. The stump healed and the individual did not appear to be inconvenienced by the loss. Parturition as observed in these specimens has been described elsewhere (see Morrison, 1946).

The rate of oxygen consumption and water loss in Peripatus was compared to several arthropods and annelids of fairly similar size, habitat and body form: centipeds (*Lithobius*); millipeds (*Julus*); sow bugs (*Oniscus*); and earthworms. These were all collected locally with the exception of one small tropical earthworm found among the debris.

Observations

Sensory responses

With the exception of the antennae the animals showed equal tactile sensitivity all over the body, on the dorsal and ventral surfaces and on the legs. A very light stimulation could be applied with no response, a light one produced a local withdrawal of a leg or small section of the body, while a strong stimulus led to a general withdrawal. Holliday (1942) noted that fairly large wood lice and centipeds could crawl over the body of a Peripatus without evoking any response. The antennae are much more sensitive and the lightest touch here results in the retraction of one or both. With stronger or repeated stimulation the animal will completely contract and change its direction of progression; further irritation provoked the well known ejection from the slime glands. These responses are in accord with the histological findings of Manton (1937) that while a single well ensconced sense capsule was found in each primary body papilla, each antennal papilla bore at least three much more exposed capsules with much heavier innervation.

The animals usually walked forwards but when startled would often reverse their direction, apparently walking backwards with equal ease. Occasionally they would half turn backwards and then move in the form of a "U" with the legs of the anterior half walking forward and those of the posterior half walking backwards. This mode of progression must impose an interesting problem in coordination.

The response of the animals to a single point source of light (a two-cell flashlight with reflector and glass removed, at a distance of 0.5 to 1 m.) was recorded by tracing their path on a large underlying sheet of paper. A number of records were made both with the light fixed and with it moved through 90 or 180° halfway through the record. Examination of the records showed no oriented negative phototropism; indeed, the animals actually travelled towards the light more often than away from it. Thus these animals would appear to be unable to localize light but only to be aware of it. This corresponds to the observations of Manton (1938) that the movement of objects near Peripatus elicited a response only when accompanied by air movement. These experiments were not carried out in a saturated environment, however, and it is possible that with the very strong stimulus of dryness removed, some phototropic pattern might be observed.

Water balance

In measuring water loss the animals were placed in large ($D = 5$ cm.) flat, weighing bottles containing a layer of calcium chloride covered by a floor of brass gauze. Measurements were made at 24° which is within the range normally encountered by these species (Kenoyer, 1929), and for periods of 30 minutes. No circulation was supplied, the movement of the animals themselves providing for convection. The Peripatus were particularly uneasy in this very dry atmosphere and kept in constant and vigorous motion.

The values obtained for the two species of Peripatus and for several other animals are summarized in Table I. Water loss has been computed on the basis of both body weight, and the two-thirds power of the body weight.[3] The latter is perhaps a more reasonable basis for comparing animals of different size. The two values for Peripatus agree well and lie between those found for the annelids and arthropods. They indicate that Peripatus has a twofold advantage over the earthworm[4] in the conservation of water; and that it is at a twofold disadvantage as compared to the centiped, the most xerosensitive arthropod studied. Other arthropods showed values ranging down to one-twentieth that observed in Peripatus. These data are presented graphically in Figure 1.

Manton and Ramsay (1937) reported on water loss in Peripatus under the much more rigorous conditions of 30° with a 7 m./sec. (16 m.p.h.) wind and a rela-

[3] This quantity is proportional to the surface area in animals of similar body form. In Peripatus and the arthropods where the actual body surface is increased by appendages and papillae, loss of water very probably takes place largely through the trachae (note Mellanby, 1935). Water loss will therefore be related to respiration which is also roughly proportional to the two-thirds power of the body weight in animals of different size (Krogh, 1916).

[4] This will be a minimum figure since the body weight of the earthworm includes a considerable amount of dirt in the gut. These earthworms were kept in clean wet containers for 1½ days before use, during which time they evacuated up to 15 per cent of their weight, but more undoubtedly remained.

tive humidity of 27.5 per cent. They found a value of 13.0 mg./g. min. or 2 to 3 times our value. A similarly measured value for an earthworm was about half as large on a weight basis or of equal magnitude on the basis of surface area. However, the advisability of making measurements under physiological conditions should be stressed since under abnormal circumstances quite different relations may hold. Thus, for example, Ramsay (1935) showed that in the cockroach water was lost

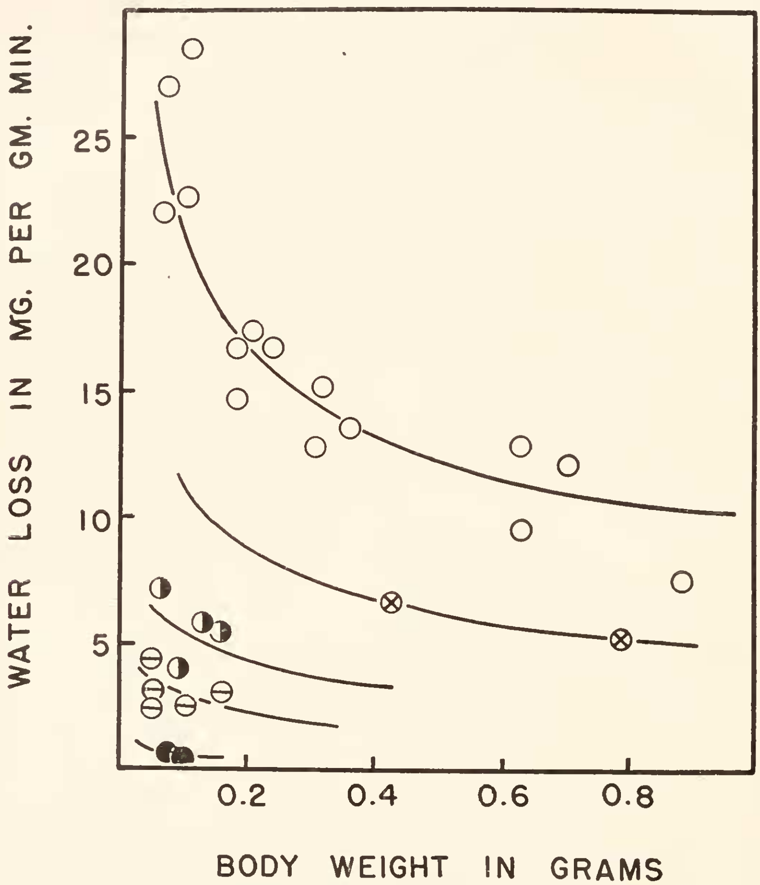

FIGURE 1. Water loss in Peripatus and other animals at 24° over calcium chloride as a function of the body weight. Open circles, earthworms; crossed circles, Peripatus; half-closed circles, centipeds; lined circles, sow bugs; closed circles, millipeds. The curves represent $Y = K\ (X)^{2/3}$, where the values for K are the average values given in Table I.

much more rapidly at temperatures above 30° with an apparent breakdown of the hydrophobic character of the body surface.

In considering this function it is of interest to note that Clark (1915) concluded on the basis of distributional and taxonomic considerations that the Onychophora had originally evolved in a cooler rather than a warmer environment. Thus, the more primitive groups are found on mountains or in the "temperate" regions while the more recent forms are tropical. This is, of course, entirely in accord with the physiological considerations since the xerotic stress would be reduced at a lower temperature and such an environment would be more favorable for evolution from an aquatic to a terrestrial mode of life.

TABLE I

Water loss in Peripatus and other animals at 24° over calcium chloride

Animal	Number and weight in mg.	Duration of experiment in min.	Water loss	
			mg./g.min.	mg./g.$^{2/3}$min.
Earthworm	884	15	7.4	7.1
	703	15	12.0	10.4
	360	15	13.4	9.6
	208	10	17.3	10.4
	105	8	22.6	10.7
Peripatus				
Epiperipatus	788	30	5.2	4.7
Oroperipatus	423	30	6.6	5.0
Centiped	150	60	5.6	3.0
	135	20	5.9	3.1
	4×95	60	4.1	1.9
	4×63	30	7.2	2.8
Sow bug	158	25	3.0	1.6
	97	40	2.5	1.2
	6×49	60	3.0	1.1
	48	20	4.5	1.6
Milliped	3×76	120	0.56	0.24
	3×98	600	0.44	0.21
Averages				
Earthworm	15 Experiments			9.9
Peripatus	2 Experiments			4.9
Centiped	4 Experiments			2.5
Sow bug	5 Experiments			1.3
Milliped	2 Experiments			0.22

Respiration

The oxygen consumption of the larger species of Peripatus and of various other animals was measured in a Warburg apparatus.[5] Carbon dioxide was absorbed in sodium hydroxide in a small cup fused to the bottom of the chamber. The animals were placed directly in the chamber and were kept from the lye by a small screen shield. Measurements were made at 25.0° C. over a period of 60 minutes.

The results on Peripatus are shown in Figure 2. After a restless initial period (10 minutes) it settled down to a very uniform rate of oxygen consumption. The centipeds, also shown in Figure 2, were less regular. The results for the various

[5] I am indebted to Dr. William Carroll for the use of his calibrated Warburg assembly.

animals are summarized in Table II. The exact significance of the "resting" or "basal" oxygen consumption is not known but some correlation between it and the "intensity" of the organism has been observed. Compared on a weight basis Peripatus consumes oxygen at the same rate as the earthworm and at about half the rate of the arthropods. It has been observed, however, that within a given group, the metabolism per unit of weight varies with the size of the animal (note Edwards, 1946, for example), and that the metabolism is more nearly proportional to some

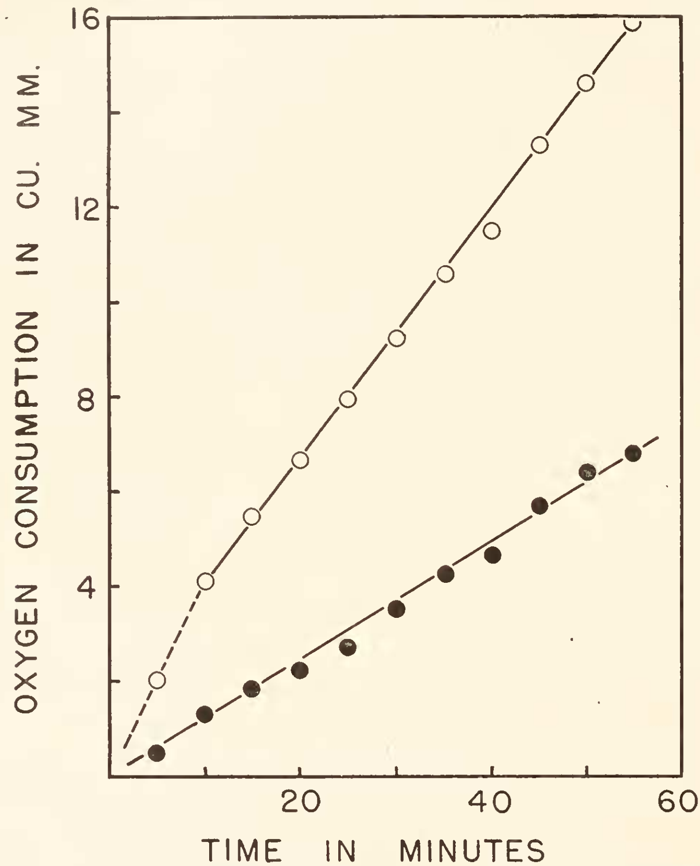

FIGURE 2. Oxygen consumption in Peripatus and the centiped as a function of time. Open circles, Peripatus (*Epiperipatus*), 0.68 g.; closed circles, 3 centipeds, total weight 0.33 g.; temperature, 25°.

lower power of the weight. As a first approximation this may be taken as the two-thirds power (Krogh, 1916). When the oxygen consumption is compared on this basis, Peripatus agrees more closely with the arthropods and has a higher value than the earthworm.

The hydrophobic character of the body surface has been noted by many observers. It is particularly evident when the animal is submerged since the body papillae hold the water away from the body surface and leave the animal entirely surrounded by a sheath of air. It would seem entirely possible that this air sheath may function as a respiratory surface under water. Such a mechanism has been demonstrated in certain aquatic insects which carry down an air supply by means of hydrophobic hairs and which, by this means, greatly extend their periods under water (Krogh, 1941; Wigglesworth, 1931). Since Peripatus must be often covered by water in rainstorms, particularly as its lack of resistance to dessication forces it to frequent wet places, this mechanism could be of real utility and have a considerable survival value. This would provide a functional explanation for the papilla-covered body surface which is characteristic and unique in the Onychophora.

TABLE II

Oxygen consumption in Peripatus and other animals at 25° C.

Animal	Weight in mg.	Oxygen consumption	
		cc./g.hr.	cc./g.$^{2/3}$hr.
Earthworm	96	0.22	0.10 [1]
Peripatus (*Epiperipatus*)	680	0.23	0.20
Millipeds	3×111	0.46	0.22
Centipeds	2×69	0.56	0.22
Pill bugs	5×61	0.35 [2]	0.14

[1] Lesser (1908) reported values of 0.4 cc. per g.$^{2/3}$hr. at 19° at which temperature the oxygen consumption should be about half that measured at 25° (Vernon, 1897).

[2] Edwards (1946) reports a similar value but at a temperature of 17°.

SUMMARY

The Onychophora represent a morphological transition between the annelids and the arthropods. They also represent a physiological transition between the aquatic and the terrestrial environment. In the latter transition the most important adaptations are those involving the functions of water conservation and respiration.

The ability of Peripatus to conserve water has been compared to that of comparable annelids and arthropods. Peripatus is shown to be intermediate to those two groups in this function, losing twice as much water as the centiped, but only one-half as much as the earthworm. This corresponds to its taxonomic and ecological positions.

The "resting" rate of oxygen consumption has also been compared to other animals. The rate in Peripatus is comparable to that in the arthropods and larger than that in the earthworm.

It is suggested that the unique papilla-covered body surface may represent an adaptation for underwater respiration to meet the environmental restriction imposed by the inadequate regulation of water loss.

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